

Interrelationships of scombroid fishes: an aspect from larval morphology*

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Abstract

Larval stages of the subfamily Scombrinae covering 12 out of 14 genera (no information are available for *Orcynopsis* and *Cybiosarda*) are studied with special reference to elucidate the intergeneric relationships chiefly on the basis of the larval morphology. A total of 13 larval characteristics were selected and each assigned to two or three coded state in the order from primitive to derived state. Using the dendrogram established on numerical basis of these larval aspects, 12 genera are separated into four groups. There are found general agreements between the groups thus obtained and the current classification of the Scombrinae, except for several points mostly associated with the problematic genera such as *Acanthocybium* and *Allothunnus*. The larval stand point also does not illustrate so clearly the intergeneric relationships among several genera of Scomberomorini and Sardini.

In some fish families, our knowledge of their larval stages have become substantial enough to make definite contribution to the understanding of relationships among genera and species, e. g., Myctophidae (MOSER and AHLSTROM, 1974). While preliminarily, the present paper also deals with the same aspect for the family Scombridae. As is well known, the larval development of this family is best studied among the oceanic fish groups; RICHARDS (1973) and GORBUNOVA (1974) presented the extensive review on the larval fish taxonomy.

So far as we know, however, pertinent literatures have been mostly concerned with the description or identification of the larvae at specific level. RICHARDS (1973) appears the first who suggested the possible generic interrelationships of some larval characteristics in association with the myomere counts. His opinion may be summarized as follows:

- Group I : *Scomber*; low myomere counts (30-31), heavier pigmentation, no preopercular spines, the first dorsal fin develops before the second dorsal fin.
- Group II : *Auxis*, *Katsuwonus*, *Euthynnus*, *Thunnus*, *Allothunnus*; moderate number of myomeres (38-43), large head, few chromatophores, similar body proportion.
- Group III : *Sarda*, *Scomberomorus*, *Acanthocybium*; high numbers of myomeres (43-65), presence of a spiny supraorbital crest, progressive increase in snout length.

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Groupings of the scombroid genera basing on the vertebral counts are followed by GORBU-NOVA (1974) with slight differences in the criterion for the latter two groups (38-41 and 45-64). OKIYAMA and UHEYANAGI (1977) may be another article discussing the generic interrelationships from the larval stand point. Brief remark of MATSUMOTO (1968) such as "size of premaxillary (in larvae) may be of generic significance (in scombroid taxonomy)" is also worthy to be mentioned. By the way, one must remember the circumstances that the adult systematics of this problematic family have been fairly well revised through the recent articles on worldwide basis such as COLLETTE and CHAO (1975), which facilitated the present research. We essentially follow the systematics of COLLETTE and CHAO (1975) in the following discussion but subfamily Gasterochisminae is not included here because of the complete lack of available information*.

To date, early life histories have been published for 12 out of 14 genera of the subfamily Scombrinae (Table 1) with varying degree of available information; developmental stages are unknown for *Cybiosarda* and *Orcynopsis*, whereas RICHARDS (1973) again suggested the possibility that the latter may be confused with *Sarda*. For several speciose genera such as *Scomberomorus* or *Sarda*, our knowledge is yet limited to only a part of the developmental stages or a part of the congeners, so that generic diagnosis for their larval characteristics are tentatively defined herein on rather common representatives. The specific interrelationships within the same genus will be mentioned little in this article.

Fig. 1 illustrates the similar stage specimens representing the 12 genera. In view of the most diverse nature in the external morphology as well as the best known stages for most elements, well advanced postlarvae or early juveniles are reproduced here. In the following analysis of interrelationships, where the approach set forth by EBELING and WEED (1973) is employed with slight modification, characteristics in these stages are highly appraised. We selected a total of 13 larval characters to find the generic interrelationships by consulting the previous contributions such as RICHARDS (1973) and OKIYAMA and UHEYANAGI (1977). As can be seen in Table 2, two or three codes are established for all these characters with the presumed directional sequence from the primitive to derived character state. The order of the character index does not imply a sequence of any phyletic importance. Definition of these coded state is not an easy task in several cases because of the incomplete descriptions of the specimens or the indistinguishable state of characters. For example, the pterotic spine in *Allothunnus*, and the spiny supraorbital crest and jaw development in *Scomberomorus* provide problems bearing on this latter case. We assigned the lower coded state for them. Contrary to the expectation of RICHARDS (1973), pigmentation patterns for which information are available most frequently can not be so useful in establishing the adequate coded states at generic level. Therefore, two pigmentation characteristics included here are the results of highly sub-

* RICHARDS (1973) stated that *Gasterochisma* is probably not a scombroid without giving further remarks.

Table 1. Present status of the larval fish taxonomy of the family Scombridae. Systematics are due to COLLETTE and CHAO (1975).

Subfamily, tribe, and genus	Genus no.	Present state of the larval fish taxonomy	
		generic level	species level
Gasterochisminae			
<i>Gasterochisma</i>	0	no information	no information
Scombrinae			
Scombrini			
<i>Scomber</i>	1	well established	well established
<i>Rastrelliger</i>	2	well established	rather well established
Scomberomorini			
<i>Grammatorcynus</i>	3	well established	no problem in identification but poor information
<i>Scomberomorus</i>	4	well established	incomplete or none for many species
<i>Acanthocybium</i>	5	well established	well established
Sardini			
<i>Orcynopsis</i>	6	no information	no information
<i>Cybiosarda</i>	7	no information	no information
<i>Sarda</i>	8	rather well estab- lished	no problem in identification but poor information
<i>Gymnosarda</i>	9	well established	well established
<i>Allothunnus</i>	10	well established	well established
Thunnini			
<i>Auxis</i>	11	well established	incomplete
<i>Euthynnus</i>	12	well established	well established
<i>Katsuwonus</i>	13	well established	well established
<i>Thunnus</i>	14	well established	problematic for several species

jective qualification. The sequential aspects of the fin development are also beyond the primary concerns in this article. Following the systematics of COLLETTE and CHAO (1975), the larval characteristics revealed by *Scomber* are considered to represent the most primitive or basic state among the scombroids in question, thus the coded state of this genus being always assigned at the lowest rank. This limitation may require the further discussion but surely has the advantage to prevent the confusion in determining the primitive and derived condition.

A set of tables (Tables 2, 3, 4) shows the steps to compile the dendrogram giving the interrelationships on numerical basis (Fig. 2). For the details of this procedures, see EBELING and WEED (1973). This dendrogram demonstrates that 12 genera can be broken down into following four groups with the order from the primitive to derived.

Group A: *Scomber*, *Rastrelliger*

Group B: *Grammatorcynus*

Group C: *Allothunnus*, *Auxis*, *Euthynnus*, *Katsuwonus*, *Thunnus*

Group D: *Scomberomorus*, *Sarda*, *Acanthocybium*, *Gymnosarda*

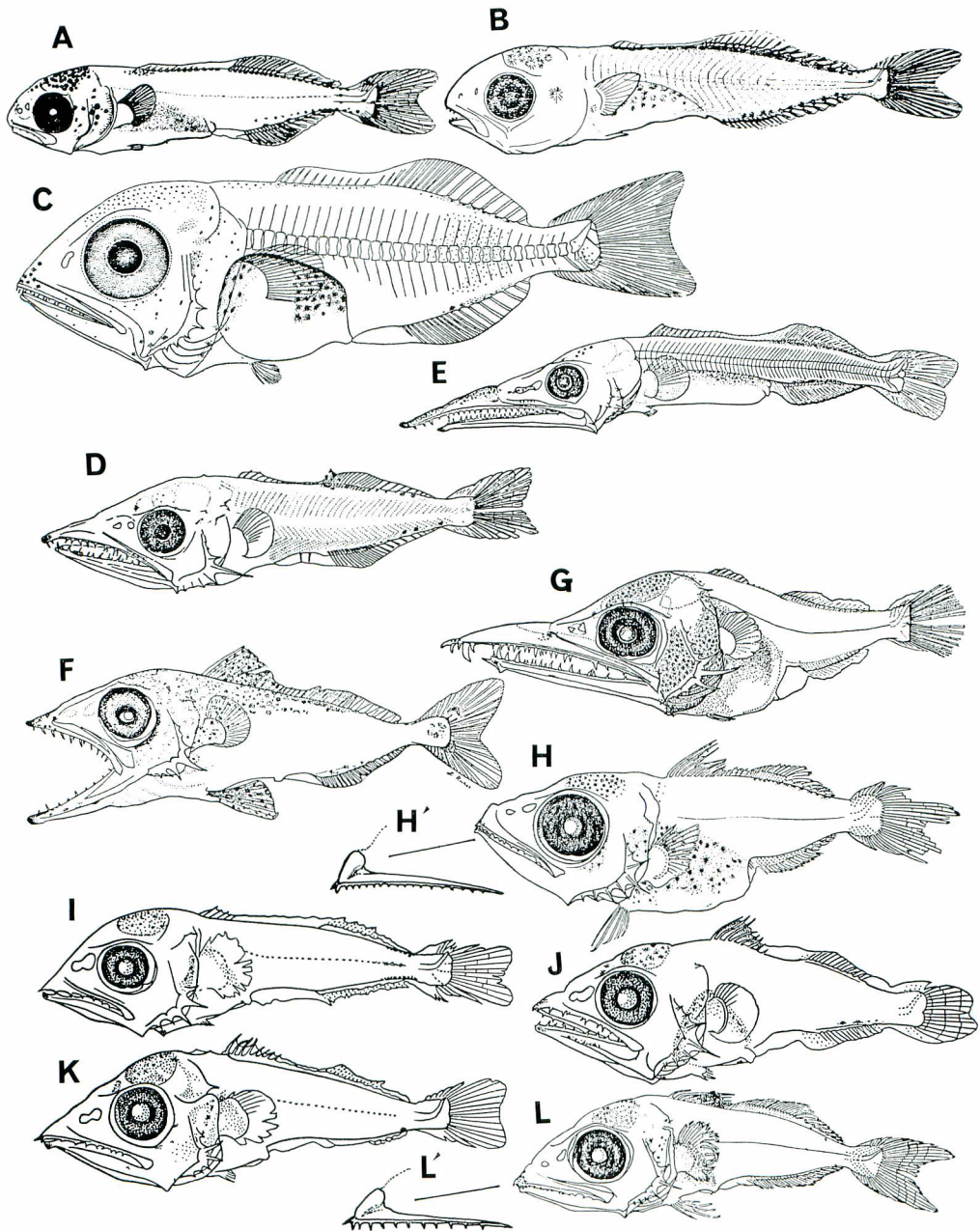


Fig. 1. Advanced postlarval or juvenile stages representing 12 genera of the subfamily Scombrinae. A, *Scomber japonicus*, 11.8 mm in TL (Uchida *et al.*, 1958): B, *Rastrelliger brachysoma*, 11.8 mm in TL (Boonprakob and Dhebtaranon, 1972): C, *Grammatorcynus bicarinatus*, 8.5 mm in SL (?) (Wade, 1951): D, *Scomberomorus cavalla* 10.0 mm in SL (Wollam, 1970): E, *Acanthocybium solandri*, 10.7 mm in SL (Matsumoto, 1967): F, *Sarda chiliensis*, 16.7 mm in FL (Pinkas, 1961): G, *Gymnosarda unicolor*, 9.06 mm in SL (Okiyama and Ueyanagi, 1977): H, *Allothunnus fallai*, 8.7 mm in TL (Watanabe *et al.*, 1966): I, *Auxis* sp. 8.7 mm in TL (Nankai R. F. R. L., 1964): J, *Euthynnus affinis*, 7.6 mm in TL (Nankai R. F. R. L., 1964): K, *Katsuwonus pelamis*, 7.8 mm in TL (Nankai R. F. R. L., 1964): L, *Thunnus thynnus*, 10.3 mm in TL (Yabe *et al.*, 1966). H' and L' indicate premaxillary bones of pertinent species.

Table 2. Presumed phylogenetically important larval (chiefly advanced postlarval or early juvenile stages) characters as coded state for comparison of 12 genera of the subfamily Scombrinae.

Character index	Character	Coded state		
		1	2	3
1	Supraoccipital spine	absent	—	present
2	Head	small; less than 1/3 of SL	—	large; more than 1/3 of SL
3	Viscera and vent	compact with wide space from Af	—	elongated, with vent just in front of Af
4	Snout	rounded	pointed	elongated
5	Premaxillary teeth	minute	large	large; some fang-like
6	Jaw	equal size	equal or unequal size	unequal with distinct upper jaw projection
7	Preopercular spine	absent	—	present
8	Spiny supraorbital crest	absent	present or absent	present
9	Pterotic spine	absent	—	present
10	Cartilaginous pad on lower jaw	absent	present or absent	present
11	Dorsal body pigmentation	heavier	—	lighter
12	Post vent pigmentation	present, extensive	absent or a few dots	absent
13	Myotome counts	low; 30-31	middle; 38-41	high; 40-65*

* Exceptional low vertebral count of *Scomberomorus sinensis* is responsible for this unclearly discreted coded state.

Table 3. Comparison of 12 genera of the subfamily Scombrinae. For the figure of 13 characters and their coded state, see Table 2.

Genus	Coded character states by character number													total score
	1	2	3	4	5	6	7	8	9	10	11	12	13	
<i>Scomber</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	13
<i>Rastrelliger</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	13
<i>Grammatorcynus</i>	1	3	1	2	1	1	3	1	1	1	1	1	1	18
<i>Scomberomorus</i>	3	3	1	3	2	2	3	2	2	2	1	1	3	28
<i>Acanthocybium</i>	1	3	3	3	2	3	3	1	3	3	3	1	3	32
<i>Sarda</i>	1	3	1	3	2	2	3	3	3	1	3	1	3	29
<i>Gymnosarda</i>	1	3	1	3	3	3	3	3	3	3	3	3	2	34
<i>Allothunnus</i>	1	3	1	2	2	1	3	1	1	1	3	3	2	24
<i>Auxis</i>	1	3	1	2	2	1	3	1	3	1	3	1	2	24
<i>Euthynnus</i>	1	3	1	2	2	1	3	1	3	1	3	1	2	24
<i>Katsuwonus</i>	1	3	1	2	2	1	3	1	3	1	3	1	2	24
<i>Thunnus</i>	1	3	1	2	2	1	3	1	3	1	3	2	2	25

Table 4. Number of characters having identical states between each pair of 12 genera of the subfamily Scombrinae. The characters and comparative states are listed in Tables 2 and 3.

	S	R	G	Sc	A	Sa	Gy	Ao	Au	E	K	T
<i>Scomber</i> (S)	13	—	—	—	—	—	—	—	—	—	—	—
<i>Rastrelliger</i> (R)	13	13	—	—	—	—	—	—	—	—	—	—
<i>Grammatorcynus</i> (G)	10	10	13	—	—	—	—	—	—	—	—	—
<i>Scomberomorus</i> (Sc)	3	3	5	13	—	—	—	—	—	—	—	—
<i>Acanthocybium</i> (A)	3	3	5	6	13	—	—	—	—	—	—	—
<i>Sarda</i> (Sa)	4	4	6	8	9	13	—	—	—	—	—	—
<i>Gymnosarda</i> (Gy)	2	2	4	4	8	8	13	—	—	—	—	—
<i>Allothunnus</i> (Ao)	6	6	9	4	6	7	7	13	—	—	—	—
<i>Auxis</i> (Au)	6	6	9	5	8	9	7	11	13	—	—	—
<i>Euthynnus</i> (E)	6	6	9	5	8	9	7	11	13	13	—	—
<i>Katsuwonus</i> (K)	6	6	9	5	8	9	7	11	13	13	13	—
<i>Thunnus</i> (T)	5	5	8	4	7	8	7	11	12	12	12	13

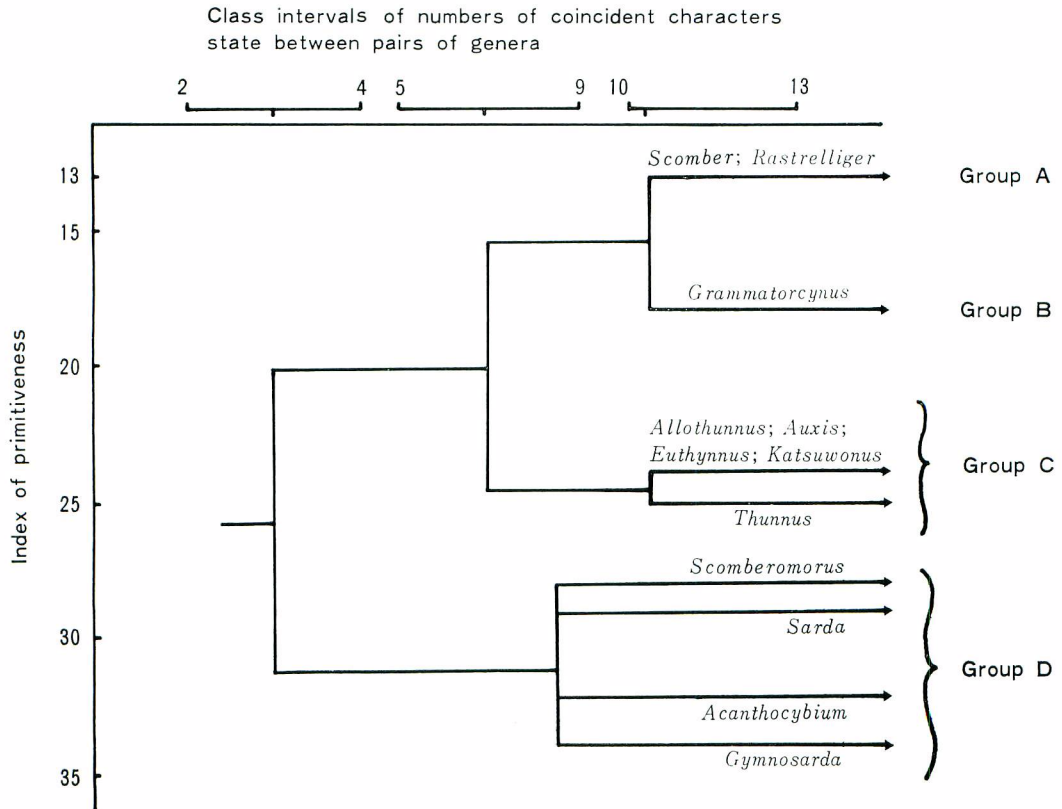


Fig. 2. Numerically constructed dendrogram depicting larval morphological relationships among 12 genera of the subfamily Scombrinae. For detailed explanation see Ebeling and Weed (1973).

Although the lowest ranking of *Scomber* by means of "index of primitiveness" is a natural result, its complete duplication with *Rastrelliger* is rather astonishing. The complete lack of spinous head armatures clearly demarcates them from other scombroids. Group A, therefore, forms a distinct and uniform assemblage well corresponding to the tribe Scombrini of COLLETTE and CHAO (1975) as well as Group I of RICHARDS (1973). Group B comprises a sole genus, *Grammatorcynus*, with a unique larval feature, although a description of the early larvae and juveniles by WADE (1951) includes only rather advanced stages. In several aspects, they show a close resemblance with Group A, but development of preopercular spines coupled with large head will clearly demarcate this genus from group A. Nevertheless, overall larval evidence appears to provide little possible indication as to its systematic position in Scomberomorini currently established (COLLETTE and CHAO, 1975).

Group C is another closely knit assemblage revealing the complete agreement with Group II of RICHARDS (1973). In view of the fact that genera of this assemblage cover three out of four ecological groups defined by the nature of distribution (SHUBNIKOV, 1974), these larval morphological uniformity must be highly evaluated from the phylogenetical point of view. A problem arises as to the allocation of *Allothunnus*, since COLLETTE and CHAO (1975) referred this genus to tribe Sardini instead of Thunnini, despite "the presence of prootic pits" in *Allothunnus* suggestive of its possible association with Thunnini. Indeed, larvae of this genus bear peculiar features such as "the absence of pterotic spine" or "a distinctive protuberance at the end of the snout". As mentioned elsewhere in this paper, this first character deserves further consideration but there is, we believe, clear difference in the degree of development of this spine between *Allothunnus* and other genera of this group. For the latter one, there is a supposition that it may be an artifact caused by dehydration of the specimen (RICHARDS, 1973). As is shown in Fig. 1, however, such is not likely the case. Even through this characteristic suggests its unique systematic position, no definite conclusion can be reached from these overall larval evidences that *Allothunnus* has closer association with Sardini rather than Thunnini. We are still in favour of our larval integrity.

Except for *Gymnosarda*, generic composition of Group D shows good correspondence with Group III of RICHARDS (1973). Judging from the critical revision by COLLETTE and CHAO (1975), current groupings are likely rather forced. Perhaps, "index of primitiveness" is primarily responsible for this confusion. It simply indicates the specialized level of the pertinent elements irrespective of their remote association. It seems safely be said that most specialized state revealed by larval *Gymnosarda* is associated with the adult evidence that "it (*Gymnosarda*) is very different from the other genera of Sardini" (COLLETTE and CHAO, 1975), along with its unique habitat selection (SHUBNIKOV, 1974). The possible parallel trend in the jaw development and remarkable head spination in this genus (OKIYAMA and UEYANAGI, 1977) may surely account for this highest state of specialization.

On the other hand, *Acanthocybium* is a somewhat puzzling genus. Its larvae develop the unique mosaic of the larval characteristics such as the elongated viscera peculiar to this ge-

nus on one hand, and less specialized ones such as the absence of the supraorbital spines or fang-like teeth on the extremely elongated snout on the other hand. In the sequence of dorsal fin differentiation, it is rather exceptional by the earlier development of the soft rays than the spinous portion (MATSUMOTO, 1967). Its exceptionally high numbers of the vertebrae and the unique distribution pattern might be concerned largely with this confused state of larval systematics.

Scomberomorus is also the assemblage with less clear intergeneric relationships. So far as the larval characteristics under scrutiny are concerned (Table 4), it represents the most isolated state of features, whereas there are known the most remarkable intrageneric variations in the relevant characters. If the supraoccipital spine is commonly shared by this genus as suggested by WOLLAM (1970), this characteristic would well substantiate its distinct systematic allocation within Scomberomorini. In this connection, recent revision of the tribe Scomberomorini by DEVARAJ (1975) is worthy to be mentioned, since it revealed that *Scomberomorus* is one of the most distinct genus among the scombroid fishes with possible close affinity with *Acanthocybium* and furthermore *Scomberomorus* shows modification in many osteological characteristics to suit its own line of specialization towards an incomplete return to characters found in the family Carangidae. Hence, the common development of the supraoccipital crest or spine in carangid fishes as suggested by OKIYAMA (1970) is of particular interest. Contrary to the above mentioned conclusion of DEVARAJ (1975), numbers of coincident characters state between pairs of genera are distinctly greater in the pair of *Sarda* and *Acanthocybium* than in that of *Scomberomorus* and *Acanthocybium* composing the tribe Scomberomorini. This may be due to the more derived state of the two genera in the former pair than *Scomberomorus* as can be seen in the following comparison of frequencies of each coded state among the four genera of our Group D:

Coded state	1	2	3
<i>Scomberomorus</i>	3	5	5
<i>Acanthocybium</i>	3	1	9
<i>Sarda</i>	4	2	7
<i>Gymnosarda</i>	2	1	10

It is well known that myotome or vertebral counts are not only one of the most trenchant characteristics in the taxonomy of the scombroids throughout the stages, but also proved to be of significant use in considering the relationships of the scombrids including the gempylids as well as trichiurids (MATSUBARA and IWAI, 1958). The clustering of the scombroid genera by means of the graphic methods like MATSUBARA and IWAI (1958) are given in Fig. 3, where, due to COLLETTE and CHAO (1975) and DEVARAJ (1975) among others, majority of the relevant species is included. As indicated by ASANO (1977), vertebral characters of the family Scombridae are as a whole referable to ACVV type which means the abdominal and caudal vertebral number correlatedly variable type. Scrutiny of this figure, however, reveals two possible

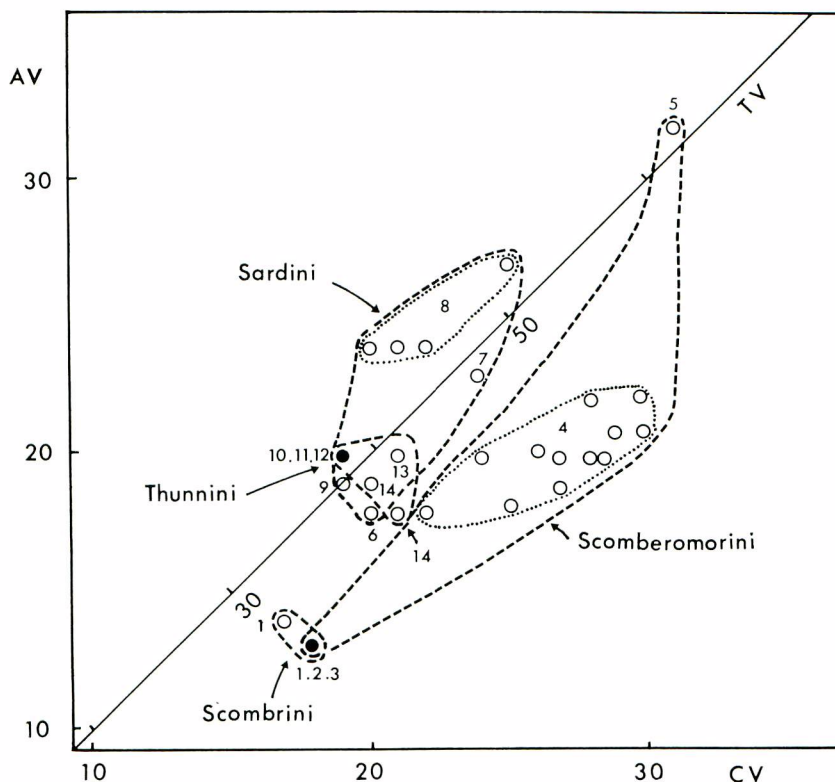


Fig. 3. Relationships between the numerical characters of vertebrae (AV, abdominal vertebrae; CV, caudal vertebrae) and four tribes of the subfamily Scombrinae established by Collette and Chao (1975). Only typical counts are included here and closed circles indicate the duplication of the same numbers by different genera. Figures attached to circles show the genus number given in Table 1. For *Scomberomorus* and *Sarda* with various combination of vertebral counts, generic boundary is given by dotted line.

lines of evolutionary trends in the pertinent characters in terms of AV: CV in relation to the total vertebrae. One corresponding with the change from $CV > AV$, through $AV \approx CV$ to $CV < AV$, comprises Scombrini, Thunnini and Sardini in this order. The other comprises only Scomberomorini bearing $AV < CV$ relationship over the considerable range of vertebral counts with the exception of *Acanthocybium*. It is worthy to mention that former line seems to coincide with the results of our larval standpoint, namely, Group A, B are $AV < CV$ type, Group C is $AV \approx CV$ type and Group D being $AV > CV$ type respectively. Also of worthy to note in this regard is that *Acanthocybium* agrees rather well with this line, whereas *Gymnosarda* provides no clue bearing on its most specialized larval morphology in this figure. Although we are needed the further larval study for the speciose genera such as *Scomberomorus* or *Sarda* along with the unworked genera including *Cybiosarda* and *Orcynopsis*, to substantiate these discussion, it may safely be said that our Group D is a heterogeneous assemblage and

some specialized larval features shared in common especially by *Acanthocybium* and *Gymnosarda* are the results of the larval convergence.

As a whole, our larval study revealed reasonable agreement with adult classification currently accepted (COLLETTE and CHAO, 1975), with several questionable aspects probably associated with a matter of convergence. Of interest is that both of these standpoints provided similar confusion as to the systematic position in several problematic genera such as *Acanthocybium* and *Allothunnus*. Besides these approach at generic level, intrageneric inquiries may deserve the future study in similar attempts, because the larval characteristics become evidently diversified in the speciose genus such as *Scomberomorus*.

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サバ型魚類の類縁関係に関する稚仔魚形質からの一考察

沖山宗雄・上柳昭治

要 約

サバ型魚類のサバ亜科に属する14属のうち知見のない *Orcynopsis* と *Cybiosarda* を除く12属について、主に稚仔魚の形態的特徴に基づき類縁関係を考察した。13の稚仔魚形質を選びそれぞれを、マサバ属 *Scomber* がもっとも原型に近いとの仮定のもとに、原型から特化型への序列をもった2ないし3の段階に位置づけし、大まかな数量的評価を加えた。これらの結果から、12属は4群に大別されたが、これは既往の分類体系ともよく一致することが判明した。しかし、カマスサワラ属 *Acanthocybium* やアロツナス属 *Allothunnus* のように成魚の分類においても問題点の多い属では、稚仔魚形質の面でも、類縁関係が不明瞭であるという興味深い対応が認められた。サワラ族とハガツオ族における属間関係が今回の稚仔魚研究からはあまり明瞭に描くことはできなかった。